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XIV.

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF THE MUSEUM OF HARVARD UNIVERSITY.

VII. — ON CERTAIN CULTURES OF GYMNOSPORANGIUM, WITH NOTES ON THEIR RŒSTELIÆ.

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Presented December 8, 1886.

IN a paper entitled "Notes on some Species of Gymnosporangium and Chrysomyxa of the United States," communicated to the Academy in February, 1885, Prof. Farlow gave an account of certain cultures conducted by him with a view to determine the relation of the species of *Gymnosporangium* found in this vicinity to the different *Rœsteliœ* growing in the same locality; and it is the object of the present paper to supplement these observations by an account of further experiments on the subject undertaken by the writer while studying in Prof. Farlow's laboratory during the past spring.

The more important results obtained have already been published in an article read by Prof. Farlow before the American Association for the Advancement of Science, at Buffalo, and contained in the September number of the Botanical Gazette; yet a somewhat more detailed account may be of interest, together with some further observations on the species of *Rœstelia* which may serve to explain several doubtful points in this connection. As a guide also to those unacquainted with the cycle of development of these fungi, it may not be amiss, before considering the cultures, briefly to summarize it.

The species of *Gymnosporangia*, or cedar apples as they are popularly known, are fungi parasitic upon certain cedars, — in this vicinity *Juniperus communis* and *Virginiana* together with *Cupressus thyoides* being the species attacked, — upon which they produce distortions more or less characteristic in appearance. At maturity, towards the close of spring, the fungus consists of certain sporiferous masses emerging from the distortions produced by the growth of its mycelium in the stem or leaves of the host plant. When moistened, these masses expand to many times their former size, becoming soft and gelatinous, while the spores upon their surface germinate with great rapidity. This germination consists in the growth of certain hyphæ (*promycelia*), which in turn bear laterally one or more, usually four, secondary spores, known as *sporidia;* or simply break up by the formation of transverse partitions into spore-like bodies having a similar function. These sporidia are then carried by the wind, often very considerable distances, until they come in contact with certain *Pomeæ* which furnish conditions for the further development of the fungus. In case these conditions are not supplied, the production of secondary sporidia serves as a further means of dissemination.

Having fallen upon a proper host, the sporidia produce the next phase of development by germinating, and entering the tissues of its leaves, fresh shoots, or fruit. A slight discoloration of the part affected ensues, followed by the production of flask-shaped cavities opening upon its surface known as *spermogonia*, within which are formed minute bodies, the *spermatia*, of doubtful function. These spermogonia are usually accompanied by bright orange discolorations, and by the secretion of a viscous saccharine substance attractive to insects.

The next step in development consists in the formation of *æcidia*, which appear upon the under surface of the leaves directly opposite the spermogonia, or in the same position with them if the part affected is a young shoot or fruit. The æcidia are cup-shaped bodies, within which numerous spores are produced successively, being pushed out in a mass surrounded by a membranous envelope, the *peridium*. By the rupture of this membrane the spores escape, and, carried by the wind to a proper host, produce upon it the *Gymnosporangia* from which they were originally derived. This completes the round of development, which may be summarized as follows: the *Gymnosporangia* on cedars produce spores (*teleutospores*), and these in turn produce sporidia, which, falling upon various *Pomeæ*, result in the formation of a *Rœstelia*, producing æcidial spores, which serve to reinfect the cedars with *Gymnosporangia*.

To trace this connection directly by actual experiment under test conditions was the object of the present cultures, and for this purpose seedlings and older plants of the following species were employed, viz.: *Cratægus tomentosa* and *coccinea*, *Pyrus malus*, *arbutifolia*, and *Americana*, with *Amelanchier Canadensis*. The plants were potted in most cases before the leaves were developed, towards the end of April, and kept in my rooms in Boston until the middle of July, at which time the more important results of the experiments had been reached. The locality was especially favorable for the purpose, being some miles from the nearest cedars, and this, together with the fact that only such leaves and shoots were infected as had developed after the plants were brought to Boston, went far to diminish the chance of accidental infection from outside sources.

Four rooms were at my disposal, and it was thus possible to guard against any mixture of the *Gymnosporangia* employed. A number of control plants were also used, and, by making the intervals between successive sowings sufficiently great, plants subsequently infected were made to serve a similar purpose. The *Gymnosporangia* used included all the species found in this vicinity; namely, *macropus*, *clavariæforme*, *globosum*, *biseptatum*, *Ellisii*, *clavipes*, and *conicum*. All of these, with the exception of *Ellisii*, mature at about the same time, generally during the first week in May; and a supply of branches bearing the distortions peculiar to the various species was gathered in April, before the sporiferous masses had been protruded by rains, and kept apart in water for the subsequent sowings.

The method of infection was as follows. Unexpanded sporiferous masses were put in watch-glasses with a little water, and these placed in a moist chamber, a common jelly tumbler filled with wet *sphagnum* being found convenient for this purpose. In from twelve to eighteen hours the teleutospores had as a rule produced an abundance of sporidia in the water and on the surface of the expanded masses. The latter were then torn apart, and placed directly upon the plants to be infected, which were first thoroughly sprinkled, and after infection kept, when practicable, under bell jars or cones of wet paper for about twenty-four hours; after which they were uncovered and repeatedly sprinkled. The results obtained seemed better where portions of the jelly were applied, than when water with sporidia in suspension was employed; but in the former case it is necessary to remove the dried membrane that remains, which otherwise injures the tender leaves.

In view of the theory that the spermatia are sexual in function, and fertilize a female organ, the *trichogyne*, which subsequently gives rise to the æcidium, a "fertilization" was attempted by collecting the exudations from the spermogonia in a drop of water, and painting them upon the under side of different leaves in plants infected by the same species. This was carefully followed up with *G. globosum*, without resulting in the production of any æcidia, and in two instances where æcidia were obtained (*G. biseptatum* and *macropus*) no such fertilization was attempted, thus giving no definite result for or against the sexual theory. It should be mentioned that small flies were repeatedly observed feeding on the secretions of the spermogonia; yet as these are usually confined to the upper surface of the leaves, it is difficult to understand the agency of such insects in fertilizing a female organ borne supposedly on the under side.

Turning now to the individual cultures my results with the different species were as follows.

G. MACROPUS.

April 30. Sporidia sown on
3 *Pyrus Americana.*
4 *Pyrus malus.*
3 *Cratægus coccinea.*

May 11. No result. All the plants reinfected, and in addition
2 *Amelanchier Canadensis.*
1 *Pyrus arbutifolia.*

May 13. Spots with spermogonia appeared on single leaves of two apples; but being questionable, the leaves were cut off.

May 22. Spermogonia appeared abundantly on two apples.

May 28. Two additional plants of *Pyrus malus* infected, on which spermogonia appeared.

June 5. Sporidia sown on immature fruit of *Amelanchier*, which was kept under a bell glass.

June 12. Signs of æcidia forming on the under side of the apple leaves first infected, while the leaves of those infected May 28 withered and ultimately fell off from no apparent cause. The remaining plants yielded no result whatever.

July 10. Peridia began to show on the two apples first mentioned as affected. These developed slowly, and towards the end of July were recognizable as belonging to the *Æcidium pyratum* of Schweinitz. It did not however assume the penicillate form peculiar to this *Rœstelia* until exposed to the weather; when the peridia, formerly long and barely lacerate, were turned back in the characteristic fashion.

G. CLAVARIÆFORME.

April 30. Sporidia sown on
3 *Pyrus Americana.*
3 *Pyrus malus.*

May 11. No result, and the same plants reinfected with the addition of
3 *Cratægus tomentosa.*

May 18. Spermogonia appeared on each *Cratægus*.

May 30. Signs of æcidia on all the leaves affected, localized on the midribs and veins.

June 2. Peridia began to show, which in about a week developed a *Ræstelia*, having the microscopic characters of *lacerata* (the form subsequently spoken of as *lacerata*, x), while the peridia were but slightly lacerate and resembled those obtained from the *macropus* culture before exposure to the weather. With the remaining plants no result was obtained.

G. GLOBOSUM.

April 30. Sporidia sown on
3 *Cratægus coccinea.*
3 *Pyrus Americana.*
3 *Pyrus malus.*

May 9. Spermogonia appeared abundantly on all the *Cratægus* plants, on a single leaf of *Pyrus Americana*, and on one apple.

May 16. All plants that had not produced spermogonia were reinfected without result.

June 2. Sporidia sown on
1 *Amelanchier Canadensis.*

June 12. Spermogonia on *Amelanchier*, not in great abundance. This plant was accidentally destroyed late in June, at which time it showed no signs of æcidia, while the remaining plants affected continued to produce spermogonia until late in July, when the leaves withered and fell off.

G. BISEPTATUM.

May 30. Sporidia sown on
2 *Amelanchier Canadensis.*
1 *Pyrus arbutifolia.*

June 12. Spermogonia on both Amelanchiers, the *Pyrus* not affected. Towards the end of June there were slight indications of æcidia in most of the affected leaves. The development of the *Ræstelia* was very slow; and though the bulbous base of *R. botryapites* was recognizable in August, it was not until early in October that peridia were developed having the appearance and microscopic characters of *botryapites*.

G. ELLISII.

June 12. Sporidia sown on detached leaves of
Pyrus arbutifolia,
Cratægus tomentosa,
and kept in a moist chamber.

June 14. Sporidia sown on
2 *Amelanchier Canadensis.*
2 *Cratægus tomentosa.*

June 20. A manifest effect on the *Pyrus* leaves which, however, moulded without actually producing spermogonia.

June 23. Yellow discolorations appeared where sporidia were sown on the *Amelanchier* plants; otherwise no further result.

G. CLAVIPES.

May 11. Sporidia sown on
3 *Cratægus tomentosa.*
3 *Pyrus malus.*
2 *Amelanchier Canadensis.*
1 *Pyrus arbutifolia.*

May 22. Spermogonia appeared on both Amelanchiers, on two fresh shoots, as well as numerous leaves, and also upon a single apple leaf. No result with the remaining plants.

June 3. Signs of æcidia appeared on the young shoots of *Amelanchier*, one of which died, while the other,

June 12, produced *Rœstelia aurantiaca* in abundance. The leaves affected continued for some time to produce spermogonia, which showed a tendency to run along the veins and midrib.

G. CONICUM.

May 4. Sporidia sown on
1 *Amelanchier Canadensis.*
1 *Pyrus arbutifolia.*
3 *Pyrus Americana.*
4 *Pyrus malus.*

May 10–11. Spermogonia appeared on the *Amelanchier* and on one apple.

May 22. Signs of æcidia on most of the *Amelanchier* leaves, and,

May 31, a *Rœstelia*, apparently *R. cornuta,* was fairly well developed. No results with the remaining plants.

Such, in brief, were the results reached, and at first sight it would seem an easy matter, having obtained æcidia from five of the seven species of *Gymnosporangium*, to refer these, at least, to their respective *Ræsteliæ*. The task is, however, not so simple, for the reason that considerable confusion exists as to the identity and distinctions of the species of *Ræstelia* as they occur in nature.

Of the forms resulting from the present cultures *R. aurantiaca* and *botryapites* are unmistakable, and cannot be confounded with any other New England form, as may be said also of *R. transformans*. With the others, unfortunately, the case is different. Even with material collected out of doors it is difficult satisfactorily to separate them, either by gross appearance or microscopic characters; while a detailed examination of each species, as at present defined, is very confusing, and leads to the conclusion that the usual characterization of these species is erroneous in several respects.

The form, for instance, generally known in this country as *R. penicillata*, occurring on *Pyrus coronaria* and *P. malus*, as well as upon *Cydonia vulgaris* and perhaps *Cratægus*, described by Schweinitz as *Æcidium pyratum*, appears to have been incorrectly referred to the first-mentioned species. The European form distributed as *R. penicillata* on *Pyrus malus* and *Cratægus*, and considered by some authorities as a form of *R. lacerata*, seems to be very properly retained by Winter as distinct, under the name *Æcidium penicillatum*, and an examination of four exsiccati, (Karst. Fung. Fenniæ 295, Rabh. Herb. Myc. 788, Rabh. Fung. Eur. 1390, Erickson Fung. Scand. 75,) together with specimens from the Tyrol in Prof. Farlow's herbarium, indicates a well-marked species quite distinct from any American form known to me. The spores are as large as those of *aurantiaca*, averaging about 40 μ in diameter, while the peridial cells are very characteristic. Not only are they very large (about $120 \times 65\,\mu$), but the markings are peculiar, and consist of fine, clearly marked branching and anastomosing striæ running transversely without prominent ridges. In our form, on the other hand, the spores are smaller, about 25 μ in diameter, while the peridial cells are smaller and narrower, their average measurement being about $22 \times 80\,\mu$, and are marked by striæ running obliquely and anastomosing obscurely, the outline of the cell being broken by coarse ridges. In both species, the cells when isolated tend to become curved outwards, most conspicuously so in the American form; a fact to which is due the outward curling of the peridial lacerations resulting in the habit peculiar to both.

Turning next to *R. lacerata*, there seems to have been a confusion of forms in this instance also. The material thus named occurring in America includes at least two, and perhaps three forms; one, which for convenience we will call *lacerata, x,* is found abundantly in this vicinity and further to the eastward on the fruit, stems, and less frequently on the leaves, of *Amelanchier* and *Cratægus,* during June and July, wholly disappearing by the end of the latter month. A second form, *lacerata, y,* infests the leaves of *Cratægus,* and does not appear until early in August; while a third and smaller form, *lacerata, z,* is found abundantly on *Pyrus malus* simultaneously with it.

The first of these (*lacerata, x*) is very similar to Oersted's figure of *lacerata,* and is identical with the European *carpophila* of Bagnis, distributed in Herb. Critt. Ital. II. 732, and in Myc. Univ. 1326, while it occurs under *lacerata* in various other exsiccati on *Cratægus,* and seems undoubtedly distinct from the forms *y* and *z,* of which the first is usually considered the more typical form of *lacerata,* while the second is referred with some doubt to the same species. In general appearance it bears a superficial resemblance to *penicillata* and *pyrata;* but although the peridium tends to become finely shredded, the shreds are straight, diverging only slightly, without any tendency to curl outwards as in these species; nor is this tendency observable in single cells. The spores are large, having a diameter of about 27 μ, while the peridial cells are long and narrow, about $90 \times 16\ \mu$, the outline broken by fine, not very distinct ridges, the striæ somewhat obscure and *horizontal.*

In the forms *y* and *z,* the spores are smaller, about 20 μ in diameter, while the peridial cells are smaller and broader in proportion to their length, about $20 \times 65\ \mu$, with a tendency to a rhomboidal shape; the ridges are deep and sharply cut as a rule, with the striæ clearly marked and running obliquely in two directions; those above the median line, where the striæ are horizontal, running in a plane nearly at right angles to those below it. The two forms seem nearly identical microscopically; the spores and peridial cells of *z* are perhaps slightly smaller, but otherwise it differs from *y* only by its smaller size and faded yellow color.

It should be remarked, that, from a microscopic point of view, the *Rœstelia* obtained on *Cratægus* after sowing *G. clavariæforme* was identical with the form *x;* while in habit it resembled *y* very closely, the peridia being but slightly lacerate. It must be remembered, however, that the cultures were not exposed to the weather, being kept indoors during their whole development, and that, had they been exposed to rain and wind, a different habit might have supervened, as was the case with the *Rœstelia* obtained from *macropus,* where the penicillate habit was preceded by one very similar to that obtained in the present instance, the *Rœstelia* producing slender unbroken peridia, which became lacerate and curled backwards only after exposure for a short time to rain and wind. The same absence of any laceration was marked in the case of the *aurantiaca* culture, where the usually lacerate peridia were unbroken.

Of these three forms, the first, *x*, seems to me to be the true *lacerata,* as understood by Oersted and distributed as above mentioned. As regards the other two, no definite statement can be made. It should be noted, however, that, with the exception of a slight variation in the size of the spores, neither of these forms can be satisfactorily separated microscopically from *R. cornuta,* as it occurs in this country on *Pyrus Americana* and *Amelanchier,* or from a form with the *cornuta* habit, collected at Kittery, Maine, on *Pyrus arbutifolia,* apparently a new host for this species. Moreover, the form *y* often assumes a habit identical with the most typical *cornuta,* if somewhat more slender. This I have frequently observed at Kittery, and it is well shown by specimens collected in Massachusetts by Mr. Seymore, who has kindly allowed me to examine the *Rœsteliæ* in his herbarium. The possibility that these forms *y* and *z* are one or both *cornuta,* is a natural inference from the above facts. Yet, as already remarked, it is impossible from our present knowledge of them to consider it more than a conjecture.

Turning for a moment to my culture of *G. conicum,* it should be observed that the *Rœstelia* obtained had the typical *cornuta* habit, yet was not separable microscopically from the form *y*, while the date of development corresponds with neither, being earlier by about two months or more. This rapid development is therefore not easily explained, as the *Rœstelia* is not referable to any other form. That it was accidental is rendered more probable from the fact that I was unable to find any such *Rœstelia* during June in localities where *G. conicum* was abundant.

No microscopic examination of the spermogonia obtained was attempted, and in general they presented much the same appearance. Those from *clavipes,* however, were the least conspicuous and those from *macropus* were tinged with greenish and preceded in every case by yellowish discolorations. *G. globosum* produced the brightest and most luxuriant spermogonia of all, yet, as already stated, though appearing on four distinct hosts, they produced no æcidia, and it is impossible even to guess with what *Rœstelia* it is connected.

As regards the different species of *Gymnosporangium,* little need be said, since they are all readily separable. As stated by Prof. Farlow, *G. conicum*, previously referred to *clavipes*, must be added to our list of species. It is very common in this vicinity, forming the familiar bird's-nest distortions on *Juniperus Virginiana* appearing on the leaves and stem, and apparently identical with the European form on *J. communis*, though as yet it has not been observed upon this host in America.

G. clavipes, although a very common species in this vicinity on *J. Virginiana*, and further eastward on *J. communis*, is more likely to escape notice than other *Gymnosporangia*, from the fact that the distortion produced is inconspicuous; while the sporiferous masses, although more brightly colored than in the other species, are small and only slightly protruded when moist. The spores are characteristic, from their rounded outline and inflated pedicels, the latter as broad as the spores themselves, together with their peculiar method of germination, which takes place invariably from either extremity, as was shown by a large number of cultures in which no exception was noticed.

G. clavariæforme I have found common in this vicinity where *J. communis* occurs, and further to the eastward in great abundance; as at Kittery, where it is often difficult to find a juniper that is free from its attack. It precedes the other species in its date of maturity.

If my conclusions regarding its *Rœstelia* are correct, *G. macropus* must be regarded as autonomous, thus disposing of Schroeter's theory of its identity with *clavariæforme*, which seems, however, scarcely tenable on other grounds.

G. biseptatum appears to be common wherever *C. thyoides* occurs, and I found its distortions abundant at Greenland, N. H., near Portsmouth.

G. Ellisii, besides its well-known peculiarities of structure, differs from the other species in its date of maturity, which is later than any of the others. At Greenland, where it occurred together with the last-mentioned species, it was in the best condition for cultures about June 10, and in the vicinity of Boston perhaps a week earlier.

A comparison of the geographical range of the *Gymnosporangia* and *Rœsteliæ* in those localities where I have had an opportunity of observing them is not as instructive in indicating their relations as one might suppose, and often the reverse is true.

At Kittery, for instance, a locality on the sea-shore at the southernmost point of Maine, there is a certain correspondence, the form *lacerata*, *x*, with *clavariæforme*, and *aurantiaca* with *clavipes*, being the most abundant. *R. cornuta*, if I rightly refer to this species the form found on *Pyrus arbutifolia* and *Cratægus*, is somewhat more common than the comparative rarity of *conicum* in the same region would lead one to expect. *R. pyrata* was not observed at all, and *macropus* only in a single instance. *R. botryapites*, however, is exceedingly common, although no *Cupressus* is known to me within eight miles. *R. transformans* was not observed, but was collected at Greenland about a half-mile from the nearest *Cupressus*.

While collecting at Mt. Washington, N. H., during the last week in August of the present year, I observed spermogonia with æcidia just forming on leaves of *Pyrus Americana* along the path from the Mt. Washington carriage road to a point about half a mile below the snow arch in Tuckerman's Ravine. These developed in a moist chamber sufficiently to show the species to be *cornuta*. Later in the season Prof. Farlow found the same species of *Rœstelia* well developed upon the same host at an altitude of 2,500 feet on Mt. Moriah, both these localities being miles from any *Juniperus*. Prof. Farlow has also collected the most typical form of *cornuta* at Eastport, Maine, on the same host.

In the vicinity of Boston, the various *Gymnosporangia* are about equally common, with the exception of the *Cupressus* forms, and here also *botryapites* is far more abundant and widely distributed than the comparative infrequency of *Cupressus* localities would lead one to expect.

Despite these discrepancies, the species of *Gymnosporangia* with their *Rœsteliæ*, assuming my determination of *lacerata* and *cornuta* to be correct, may be with tolerable safety summarized as follows: —

G. conicum = *R. cornuta.*
G. clavipes = *R. aurantiaca.*
G. clavariæforme = *R. lacerata.*
G. macropus = *R. pyrata.*
G. biseptatum = *R. botryapites.*
G. Ellisii = *R. transformans* probably.
G. globosum = ?.

In closing, I must express my great obligation to Prof. Farlow for advice and assistance, as well as for the privilege of examining a large number of exsiccati without which any satisfactory results as regards the more obscure *Rœsteliæ* would have been impossible.